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Vol. 87. Part 6. Pp. 165-180, 1 fig. 27th September, 1938.

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THE

TRANSACTIONS

OF THE

ROYAL ENTOMOLOGICAL SOCIETY

OF

LONDON

World List abbreviation: *Trans. R. ent. Soc. Lond.*

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LONDON:
PUBLISHED BY THE SOCIETY AND
SOLD AT ITS ROOMS, 41, QUEEN'S GATE, S.W.7

Price 3s. 4d.

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SOME EXPERIMENTS ON THE INFLUENCE OF ENVIRONMENT UPON THE FORMS OF *APHIS CHLORIS* KOCH. (APHIDIDAE)

By Frank Wilson.

(*Assistant Research Officer, Division of Economic Entomology, Commonwealth Council for Scientific and Industrial Research, Australia.*)

With One Figure.

(Read 1st June, 1938.)

Introduction and Acknowledgements.

Aphis chloris Koch was first discovered in England by Mr. S. Garthside in 1929, when he was investigating the insect enemies of *Hypericum perforatum* L., one of the worst Australian noxious weeds. A study of the biology of this aphid has been made at Farnham House Laboratory. The present paper is an account of the results obtained from a number of experiments concerned with the factors which induce and inhibit the appearance of the different forms which occur during the course of the aphid's annual cycle.

I am indebted to Dr. W. R. Thompson, F.R.S., Superintendent of the Farnham House Laboratory, for his interest in the problem and his useful criticism during its progress. To Mr. S. Garthside my thanks are due for his frequent practical help and criticism.

Rearing Technique.

With occasional exceptions or modifications (which are indicated in the text) the lines of *Aphis chloris* described in this paper were reared on small shoots of *Hypericum perforatum* L., placed on wet blotting-paper in glass-topped tins. The aphids were transferred by a camel-hair brush to a fresh shoot twice each week. This method of rearing aphids gives satisfactory results and is much more suitable for experimental work than the usual technique of rearing on potted plants.

The Normal Life Cycle of *Aphis chloris* Koch.

The host-plants of *A. chloris* are restricted to the genus *Hypericum* (Hypericaceae) and of these *H. perforatum* L. is the usual host. This aphid has been recorded as feeding upon several other plants outside the Hypericaceae, but very probably these records are incorrect.

The annual life-cycle of *A. chloris*, as studied in Buckinghamshire, is as follows: The eggs are deposited by the oviparous females on the procumbent stems and the lowest part of the vertical stems of *H. perforatum* during October. The eggs hibernate through the winter and eclosion occurs at the end of March and the beginning of April in the following year. The fundatrices become mature a month later, and are followed by several generations of apterous viviparous females. By June the colonies have become quite large and some alate viviparous females develop; these disperse and found fresh colonies elsewhere. Although during June the alate females become quite common,

they have never been found to constitute the majority of the adult population. During July the alatae become increasingly scarce and finally disappear. The succeeding generations normally consist only of apterous viviparous females until about the middle of September, when adult males and, somewhat later, apterous oviparous females appear. Concurrently, the apterous viviparous females become rarer and very few individuals of this form are present in the field after the first week in October. Whilst many males arrive at maturity earlier than the oviparous females, the latter continue to mature after the males have all become adult, so that finally the oviparous females are more numerous than the males. Oviposition begins at the very end of September and continues throughout October, and even into November.

Unessential Nature of the Alate Form.

That the alate viviparous females do not form an essential part of the annual life-cycle is seen by the fact that a line of *A. chloris* can be reared through the cycle without any alatae arising.

Line A.

In one case a cycle of generations was reared at outdoor (shade) temperature. Six fundatrix nymphs were isolated and, on reaching maturity, the first six young deposited were isolated for the first filial generation. This procedure was repeated until the line ended. The fundatrices hatched on the 31st March and the eleventh filial generation nymphs were laid on the 19th September. In this line all individuals developed into apterous viviparous females, except in the eleventh filial generation when only males and oviparous females were obtained. This line was reared under conditions approximating to those in nature, and amphigonae appeared at the same time as in the field.

Several other lines have been reared through a complete cycle without any alatae arising, and it is clear that this form only arises under certain environmental conditions. Field observations suggest that no line of *Aphis chloris* produces alatae in more than one generation of the annual cycle. If, however, it be true that alatae arise as a result of particular environmental conditions, the continued application of these conditions should result in several generations of alatae in the same line.

Overcrowding. In the literature of factors causing the production of alatae, one of the most important factors is often said to be the " overcrowding " of aphids on the host plant, or even on a portion of it.

Line B.

The effect of overcrowding on *A. chloris* was studied by rearing a line on potted *H. perforatum* plants which had been pruned to a small size and were kept in a heated greenhouse. A fundatrix nymph was reared to maturity by 10th April and placed on a potted plant. The colony developed rapidly and winged adults began to appear on 19th May. The alatae were transferred to another plant and on the 19th June more alatae were obtained. These individuals were isolated in tins, and four generations of apterous viviparous females were reared in this way. The adults of the fourth generation were transferred on the 26th July to another plant and more alate individuals were obtained on the 23rd August. Some of these were placed on a further plant and a few alatae developed by the 15th September, but a little later in this month only amphi-

gonous individuals were present in the colony and thus the line came to an end. It may be seen, therefore, that alatae occurred in no less than four generations when the line was repeatedly subjected to overcrowding.

There can be little doubt that the factor causing the appearance of alatae is not " overcrowding " in itself, but the nutritional results of " overcrowding." These results appear to be, first, a reduction of the food supply (which is possibly accompanied by certain chemical and physical changes in the plant tissue which may affect the aphids) and, secondly, a mutual disturbance of the aphids resulting in a reduction of the rate of feeding.

Among other factors often considered to influence the occurrence of alatae are partial starvation, the treatment of the host plant with certain chemicals and the temperature at which the aphids are reared. Partial starvation may reasonably be taken to be an artificial method of obtaining the effect normally produced by overcrowding. The use of chemicals (*e.g.* magnesium sulphate), to produce alatae, appears to be effective in some cases; however, it has not been shown what connection, if any, this method has with the factors which produce alatae in nature.

In *Aphis chloris*, no temperature was found which was favourable to the alatae. In experiments described in this paper a total of 28 generations were reared at 26° C. (constant), twelve young being reared together in each generation, and no alatae appeared. In 78 generations reared at 21° C. (constant), each generation consisting of nine young reared together no alate specimens occurred; in 189 generations reared at the same temperature (twelve young reared together in each generation) only 22 alate specimens arose. At a variable temperature 114 generations were reared, each consisting of 12 individuals reared together. The average temperature, based on two-hour readings, was estimated for each generation and it was found that generations were reared at average temperatures of every degree from 12° C. to 20° C., but in all these generations only four alate specimens arose. Finally in *Line A.*, already described, where each nymph was isolated the aphids were reared at outside (shade) temperature and no alatae occurred. It might reasonably be supposed that if alatae in *A. chloris* occur as a result of some particular temperature, they would have arisen in a line reared under outdoor temperatures at the same time that alatae appeared in the field.

Since alatae will occur in several generations after " overcrowding " and since aphids reared in very small groups, whatever the temperature, very seldom give rise to any winged individuals, it is clear that " overcrowding " is the factor which produces alatae in *A. chloris*. Where alatae do occur in the experiments described below, their appearance is, in all probability, due to food-deficiency.

The Inhibition of the Amphigonous Forms.

Since the amphigonous forms arise at the same time each year, it would seem possible that their appearance is predetermined for a particular generation irrespective of environmental conditions. That this is not so is shown by the following experiments.

Line C.

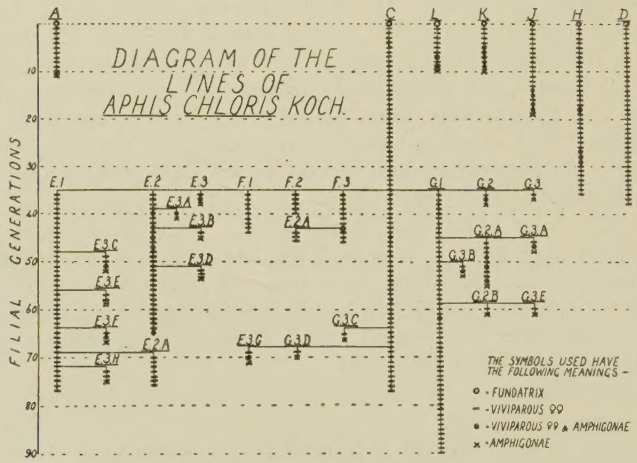
This line was reared at a constant temperature of 21° C. and was continuously exposed to electric light. The first nine nymphs laid in each generation were reared and used as parents for the succeeding generation. *Line C.* began on

the 24th March, 1933, when the fundatrix hatched, and ended on the 26th September, 1934, with the accidental death of the adults on the seventy-seventh filial generation. All adults of all these generations were apterous viviparous females. A branch of this line, started from adults of the thirty-fifth F.G. on the 11th January, 1934, was reared up to the ninety-first F.G. (see *Line G*.1. below), but the nymphs of this last generation failed to reach maturity.

Line D.

This line was reared under precisely the same conditions as *Line C.*, but the first twelve nymphs laid were reared in each generation. The fundatrix hatched on the 26th January, 1934, and the line continued for thirty-eight filial generations before the accidental death of the thirty-ninth F.G. nymphs on the 26th November, 1934, brought the experiment to an end. With the exception of one alate individual which arose in the fifth filial generation, all adults were apterous viviparous females.

It has been shown above (*Line A.*) that, under outdoor-insectary conditions, where temperature and light approximate to the conditions in nature, the amphigonae arise in the eleventh filial generation, when the earliest young



laid in each generation are used as parents for the next. *Lines C.* and *D.*, however, continued for many more generations than this without any amphigonae arising: indeed, it is very probable that had accident not brought these lines to an end, they could have been continued indefinitely. It follows, therefore, that the amphigonous forms are not predetermined for any particular generation and that the annual cycle in *A. chloris* is essentially a result of the influence of environmental forces.

The Effect of Light and Temperature.

An experiment was made on the effect of certain light and temperature conditions upon the form of *A. chloris*. The first twelve young laid in each generation (rarely a different number) were reared together and used as parents for the succeeding generation. Nine sister apterous viviparous females of the

thirty-fifth filial generation of *Line C.* were used to begin nine lines maintained under the following conditions :—

Line	Temperature	No. of hours exposure to 100-watt electric bulb each day
E.1.	21° C. (constant)	24
E.2.	,, ,,	0
E.3.	,, ,,	7
F.1.	26° C. (constant)	24
F.2.	,, ,,	0
F.3.	,, ,,	7
G.1.	Variable : lower than *E.* and *F.*	24
G.2.	,, ,, ,, ,,	0
G.3.	,, ,, ,, ,,	7

Each of these lines was exposed to daylight during a daily examination and a twice-weekly transference of the aphids to fresh shoots, but the total period of exposure to daylight would not have been greater than ten minutes a week. Otherwise all light, apart from that of the electric bulb, was excluded.

The lines were begun in the following manner. Three of the parent females were placed on a shoot of *Hypericum* and kept at 21° C. and under continuous artificial lighting. When they had laid twelve young, they were transferred to another shoot, kept in continuous darkness, and allowed to lay twelve more young under these conditions. The adults were then transferred to another shoot, which was exposed to artificial lighting for seven hours each day, and here they laid twelve more young before they were removed and killed. The *Lines F.* and the *Lines G.* were started in the same way by two other groups of three females. It is seen that the first filial generation of each line was laid under those conditions to which the line was, without intermission, subsequently subjected.

Lines E. (21° C. constant).

Line E.1. (continuous artificial light).

The young of the first filial generation were laid on the 12th January, 1934, and the line continued for forty-two generations, ending on the 26th November, 1934, by the accidental death of the adults of the last generation. In all these generations only apterous viviparous females occurred.

Line E.2. (continuous darkness).

The young of the first filial generation were laid by the 16th January, 1934, and the line continued for thirty-one generations, the nymphs of the last being killed by predatory mites on the 28th October, 1934. In the thirty generations reared to maturity, no alate females or males occurred, and the generations consisted of apterous viviparous females only, with the exception of the fifth, eighth, tenth, twelfth and thirtieth, in which a few oviparous females also arose.

Line E.2.A.

On the loss of the thirty-first generation a fresh line was begun under the same conditions, from five apterous viviparous females taken from *Line E*.1. (thirty-fourth F.G.) on the 1st October, 1934. Seven filial generations were reared and all individuals developed into apterous viviparous females.

Line E.3. (seven hours light a day).

This line continued for three generations: the first generation consisted of apterous viviparous females; the second, of apterous viviparous and oviparous females; the third, of oviparous females only. At the termination of this line, a succession of eight lines (*E*.3., *A*. to *H*.) derived from apterous viviparous females of the *Lines C*., *E*.1., and *E*.2., was reared under the same conditions. Details of the form of the adults in each generation of these lines may be found in the diagram: each line terminated within two to four generations, with the appearance of oviparous females exclusively.

Lines F. (26° C. constant).

The three lines kept at this temperature did not continue for many generations. It has been found that lines of aphids transferred to 26° C. from lower temperatures usually lose their vitality, the adults becoming smaller and more yellow in colour than is normal, and, after several generations, laying only dead or moribund young.

Line F.1. (continuous artificial light).

The young of the first filial generation were laid on the 12th January, 1934. The line continued for nine generations, the last, laid on the 8th March, 1934, failing to lay living young. The adults of all generations were apterous viviparous females.

Line F.2. (continuous darkness).

Five generations of this line were reared, the first being laid on the 13th January, 1934, and the last on the 9th February, 1934. The adults of the fifth generation did not lay any living young. In all five generations only apterous viviparous females appeared.

Line F.2.*A*.

Line F.2. having terminated, it was replaced by a fresh line kept under the same conditions and begun from adult apterous viviparous females of the eighth F.G. of *Line F*.3. Three generations of apterous viviparous females were reared, but the third generation failed to lay any young.

Line F.3. (seven hours light a day).

The young of the first filial generation were laid on the 15th January, 1934. Eleven generations were reared, the last being laid on the 19th March, 1934, but as the adults of this generation did not lay living young the line ended. With the exception of the eighth filial generation, in which six apterous viviparous females and four oviparous females were obtained, all adults were apterous viviparous females.

Lines G. (temperature variable; lower than *E*. or *F*.).

Thermographic records were kept of the temperatures at which *Lines G*. were maintained. Below are given for *Line G*.1. an average temperature for the whole period and for *Lines G*.2. and 3., average temperatures for each generation. These averages are based on two-hour readings.

*Line G.*1. (continuous artificial light).

The young of the first filial generation were laid on the 12th January, 1934. The line continued for fifty-six generations, the last being laid on the 19th September, 1935, but the individuals of this last generation died before reaching maturity. With the exception of the twenty-seventh F.G., when nine apterous viviparous females and two oviparous females were obtained, all generations consisted of apterous viviparous females only. The average temperature for the whole period was 17° C.

*Line G.*2. (continuous darkness).

This line continued for three generations, the first consisting of apterous viviparous females, the second of apterous viviparous and oviparous females, and the third of oviparous females only. These generations were reared at 15, 15 and 13° C. respectively.

Since the *Line G.*2. had ended rapidly, two other Lines (*G.*2.*A.* and *G.*2.*B.*) were reared under the same conditions. Details of the forms arising in each generation are given in the diagram. In *G.*2.*A.* generations were reared at average temperatures ranging between 17 and 20° C., and oviparous females exclusively appeared only in the ninth filial generation. In *G.*2.*B.*, on the other hand, the second generation consisted of oviparous females only, the two generations having been reared at average temperatures of 14 and 13° C.

*Line G.*3. (seven hours light a day).

This line ended after two generations, both being reared at an average temperature of 15° C. The first generation consisted of apterous viviparous females and the second of oviparous females.

Five more lines (*G.*3.*A.* to *E.*) were reared under the same conditions. The forms arising in each generation of these lines are given in the diagram. In all cases the lines ended with the appearance of oviparous females exclusively, either in the second or third filial generation. The average temperature (° C.) at which each generation was reared was :

*G.*3.*A.*	...	...	17, 18, 19.
*G.*3.*B.*	...	...	20, 20, 19.
*G.*3.*C.*	...	...	18, 19.
*G.*3.*D.*	...	...	19, 15.
*G.*3.*E.*	...	...	14, 12.

In the preceding experiment, the *Lines E.*, *F.*, and *G.*, were maintained in an approximately identical environment apart from the factors of light and temperature. Since all specimens used were of the same pure line, the difference in the results obtained may be referred directly to differences of temperature or light-exposure. If the lines be arranged in the following manner :

*E.*1.	*E.*2.	*E.*3.
*F.*1.	*F.*2.	*F.*3.
*G.*1.	*G.*2.	*G.*3.

a horizontal comparison shows the influence of light-exposure and a vertical comparison the influence of temperature.

An examination of *Lines E.*1., 2. and 3. shows that at 21° C. aphids under continuous lighting were completely of the apterous viviparous form; in

complete darkness they remained chiefly apterous viviparous females, but exhibited a marked tendency to the production of oviparous females in several generations; with a light exposure of seven hours, the aphids rapidly changed into oviparous females. *Lines F*.1., 2. and 3. show that at 26° C. only apterous viviparous females occurred under conditions of continuous lighting and continuous darkness, whilst even under seven hours light exposure, in only one generation did a few oviparous females appear. An examination of *Lines G*.1., 2. and 3. shows that at the lowest temperature with continuous lighting, the aphids were all apterous viviparous females with the exception of two oviparous females produced in one generation; with continuous darkness the line changed more or less rapidly into oviparous females; with seven hours light the aphids soon became entirely oviparous females. It should be noted that in *Lines G*.2. and *G*.2.*B*. when the average temperatures are low the change is rapid, whilst in *Line G*.2.*A*. where the temperature is relatively high, the change is slow.

From these results it is clear that continuous lighting inhibits, the seven-hours light exposure greatly encourages, and continuous darkness encourages to a lesser degree, the appearance of the oviparous form: further, that the highest temperature inhibits the appearance of the oviparous form (almost completely even under the most favourable light conditions for this form), the lowest temperature encourages the appearance of the oviparous form (even to a slight extent when the light conditions are most unfavourable), whilst the medium temperature holds an intermediate position, being able to produce 100 per cent. oviparous females under seven hours light (unlike the highest temperature), but unable to do so under conditions of continuous darkness (unlike the lowest temperature).

The preceding experiment shows clearly that temperature and light exposure are two extremely important environmental factors influencing the form of *A. chloris*; high temperatures and long hours of light exposure result in a line remaining of the apterous viviparous form, the low temperatures and short hours of light exposure cause the appearance of the oviparous form: further, that these two factors are closely inter-related, so that the effect of a certain temperature cannot be judged without taking the light conditions into account and *vice versa*.

A Light-Temperature Experiment on Lines Starting from Fundatrices.

In the previous experiment, the effect of certain light and temperature conditions was investigated on pure line aphids, which were many generations from the fundatrix. It is possible, however, that if lines newly founded by fundatrices are subjected to these conditions, the same results may not be obtained. To investigate this matter lines of *A. chloris* begun from four fundatrices were subjected to the four conditions previously found to be most favourable for the production of the oviparous females. The conditions were as follows:

Line H.: 21° C. (constant); continuous darkness.
Line J.: A lower, variable temperature; continuous darkness.
Line K.: A lower, variable temperature; seven hours light a day.
Line L.: 21° C. (constant); seven hours light a day.

The rearing technique, the number of young reared in each generation, and all other details were precisely the same as those already described for *Lines E*.2.

and 3., and *G*.2. and 3.; each line was subjected to its own conditions of light and temperature from the time the fundatrix hatched.

Line H. (21° C.; continuous darkness).

The fundatrix hatched on the 19th January, 1934. The line was continued for thirty-six filial generations, but the nymphs of the thirty-seventh filial generation, laid on the 23rd November, were accidentally killed. In all except four of these generations only apterous viviparous females occurred. The four exceptions (eighteenth, twenty-seventh, twenty-eighth and twenty-ninth filial generations) yielded both apterous viviparous and oviparous females.

Line J. (variable temperature; continuous darkness).

The fundatrix hatched on the 22nd January, 1934, and nineteen filial generations were reared. In filial generations 1 to 13 and 16, all aphids were apterous viviparous females, except for two alate viviparous females. These latter were not used as parents for the succeeding generation. In the fourteenth, fifteenth, seventeenth and eighteenth filial generations both apterous viviparous and oviparous females were obtained. The last generation yielded oviparous females only. The average temperatures at which these nineteen generations were reared (based on two-hour readings) were :—14, 14, 14, 14, 15, 16, 18, 16, 17, 18, 18, 19, 19, 20, 20, 19, 19, 18 and 20 (°C.) respectively.

Line K. (variable temperature; seven hours light a day).

The fundatrix hatched on the 2nd February, 1934. Ten filial generations were reared. In filial generations 1 to 4, only apterous viviparous females occurred; in 5 to 9 apterous viviparous and oviparous females (with one alate viviparous female arising in F.G.6. and F.G.7., these not being used as parents); whilst in the last generation only males and oviparous females were obtained. The average temperatures at which these ten generations were reared were :— 13, 14, 14, 14, 15, 18, 16, 16, 18 and 18 (°C.) respectively.

Line L. (21° C.; seven hours light a day).

The fundatrix hatched on the 2nd February, 1934, and ten generations were reared. Apterous viviparous females only were obtained in filial generations 1, 2, 4, 5 and 8. In the third F.G. all adults developed into alate viviparous females. The sixth F.G. adults consisted of apterous and alate viviparous females, and the seventh F.G. of apterous and alate viviparous females and oviparous females. The ninth F.G. yielded apterous viviparous and oviparous females, whilst the last generation consisted of oviparous females only. The alatae obtained in the sixth and seventh filial generations were not used as parents.

This experiment confirms some of the results of the preceding experiment. Here, also, the lower (variable) temperature is more favourable than 21° C. to the oviparous females, producing only amphigonae in complete darkness : again, seven hours light exposure is more favourable than continuous darkness to the amphigonae, since it can produce the latter exclusively both at 21° C. and at the lower temperature.

Reference to the data given above shows that *Line E*.2. continued for thirty-one generations and the corresponding *Line H.* for thirty-six generations, and that in both cases occasional amphigonous individuals arose without

100 per cent. oviparous females ever being obtained. The only important difference between the lines is that the line started from a fundatrix first produces oviparous females in the eighteenth filial generation, whilst *Line E*.2. does so in the fifth.

Comparing the eight *Lines E*.3. with the corresponding *Line L*., whilst the former produce entirely oviparous females in two to four generations, the latter does so only in ten, having produced its earliest oviparous individuals in the seventh generation.

Whilst in *Lines G*.2., only oviparous females are produced by the third, tenth and second generations, in the corresponding *Line J*. this result is not attained until the nineteenth generation. It is important in these lines reared under a variable temperature, however, to examine the average temperatures carefully before these results are accepted as necessarily significant, for under conditions of continuous darkness the temperature is of paramount importance. Reference to the temperatures given above, however, shows that the *Line J*. was reared at an average temperature below that of *Line G*.2.*A*., and, further, that the first six generations of *Line J*. were reared at about the same average temperature as *Line G*.2.

In the six *Lines G*.3., 100 per cent. oviparous females were obtained in two or three generations, whilst in the corresponding *Line K*. the same result was attained only in the tenth, the first individuals of this form occurring in the fifth generation.

The comparison of results obtained in the corresponding lines of these two experiments shows that whilst the same results are finally attained, many more generations are required in the lines starting from fundatrices. It appears, therefore, that there is a factor influencing the form of *Aphis chloris* which is connected with the number of generations from the fundatrix of the individuals concerned. This factor completely inhibited the appearance of the oviparous females in the earlier generations of *Lines K*. and *L*., but was gradually overcome by the environmental conditions until only amphigonae were produced.

"Generation from Fundatrix" Factor.

Whatever may be the precise nature of the "generation from fundatrix" factor, it appears that a method of inhibiting the early appearance of the amphigonae is essential to the cycle, for if the form of the aphid was purely dependent upon the light-temperature complex, it is very probable that the short day-length and low temperatures encountered by the species during April, at the very beginning of the annual cycle, would result in the immediate appearance of amphigonae. It is probable, too, that this factor prevents the early appearance of amphigonae in colonies situated in abnormally dark positions; for example, some colonies occur on the roots of the host well below soil level.

In *Lines K*. and *L*., which were subjected to conditions extremely favourable to the amphigonae, the "generation from fundatrix" factor prevented their exclusive appearance until the tenth F.G. Consequently this result (compare with *Line A*.) was attained only one generation earlier than would occur under natural conditions. In all these lines, however, each generation consisted of the earliest-laid young. It has been estimated that in *Line A*., had each generation consisted of the last-laid young, the line would have passed only through five filial generations in the same period. In the field, therefore, amphigonae, since they arrive at approximately the same time, may be of any filial generation from the fundatrix from the eleventh to the fifth. Conse-

quently, it would appear that, although under any particular set of conditions the " generation from fundatrix " factor is seen in terms of the number of generations it delays the amphigonae, the generation in itself is of no importance, being incidental to the fact that the distance in time from the fundatrix of each amphigonous individual is approximately equal.

A more correct descriptive title for the " generation from fundatrix " factor would be the " time factor." It is possible that, although there is no absolute length of time during which the " time factor " exerts its influence, there is, for any particular set of environmental conditions, a fixed length of time during which the " time factor " is effective, and at the end of this period the filial generation of any aphid will depend upon the method adopted to obtain each generation (*e.g.*, first-laid young or last-laid).

In the absence of further data on the " time factor " it is unprofitable to enter into any lengthy speculations on its nature or mode of operation, but a few words on this subject may not be without value. From what has been said above it appears, first, that the influence of the " time factor " decreases from the fundatrix until viviparous females are able to yield 100 per cent. amphigonae; and, secondly, that it must be passed from generation to generation by some form of somatic inheritance, for any genetical form of inheritance would not permit of a decreasing influence of the " time factor " from generation to generation, in the pure line. It will be shown below that amphigonous individuals can be produced in the course of a few days from viviparous females, which would otherwise have yielded parthenogenetic offspring only. It is very doubtful if a change in the environment could directly produce a genetical change in these circumstances, and it seems probable that the environment produces some change (*e.g.*, an internal secretion) either in the parent or embryo itself, which then influences the form of the embryo. If the explanation of these phenomena is of this kind, it is quite likely that the " time factor " consists of a counter-influence of a similar nature (*e.g.*, a neutralising secretion).

The Production of Amphigonae in One Generation.

It has been seen that the application of certain environmental conditions to a line of *A. chloris* will result in 100 per cent. amphigonae in as little as two generations. It is frequently maintained that several generations are required before the application of favourable conditions can produce the amphigonous form. For example, Wadley (1931) states that in *Toxoptera graminum* Rondani, the amphigonae are not produced before the second generation, born under favourable conditions, nor matured earlier than about a month after the onset of these conditions. Indeed, this belief is inherent in the concept of a " sexuparous form," for the conditions favourable to the amphigonae must produce the sexuparae before the amphigonae can occur.

To discover whether or not amphigonous individuals could be produced in one generation in *A. chloris*, an experiment was carried out on two apterous viviparous females of the seventy-second filial generation of *Line C*. These parent females had, of course, been exposed to continuous artificial light up to the time that the experiment began, but for the first nine days of the experiment they were subjected to seven hours light a day from a 100-watt electric bulb (seventeen hours in complete darkness) and thereafter, until they died, receiving continuous artificial light. The young laid during the first nine days were reared to maturity with a daily light exposure of seven hours and the rest with continuous artificial light (*i.e.*, the nymphs were reared under the con-

ditions under which they were laid). The whole experiment was carried out at 21° C. (constant) and the usual rearing technique was employed. With occasional exceptions, the young laid by each female each day were reared separately. The results obtained are given below:—

Parent A					Parent B				
Tin No.	Young laid on	Forms of Adults			Tin No.	Young laid on	Forms of Adults		
		Apt. viv. ♀♀	♂♂	Oviparous ♀♀			Apt. viv. ♀♀	♂♂	Oviparous ♀♀
Seven Hours Light a Day									
1.	23.x.34	4	—	—	1.	23.x.34	5	—	—
2.	24.x.34	3	—	—	2.	24.x.34	3	—	—
3.	25.x.34	2	—	—	3.	25.x.34	—	—	—
4.	26.x.34	3	—	—	4.	26.x.34	5	—	—
5.	27.x.34	4	—	—	5.	27.x.34	4	—	—
6.	28/29.x.34	4	1	—	6.	28/29.x.34	3	—	—
7.	30.x.34	—	—	—	7.	30.x.34	2	—	—
8.	31.x.34	4	—	—	8.	31.x.34	2	—	—
Continual Artificial Light									
9.	1.xi.34	—	—	—	9.	1.xi.34	—	—	—
10.	2.xi.34	1	—	—	10.	2.xi.34	1	—	—
11.	3.xi.34	2	—	—	11.	3.xi.34	2	—	—
12.	4/5.xi.34	2	—	1	12.	4/5.xi.34	1	—	1
13.	6.xi.34	—	—	—	13.	6.xi.34	—	—	—
14.	7.xi.34	—	—	1	14.	7.xi.34	—	—	—
15.	8.xi.34	—	—	—	15.	8.xi.34	—	—	1
16.	9.xi.34	—	—	—	16.	9.xi.34	1	—	1
17.	10/12.xi.34	1	—	—	17.	10/12.xi.34	2	—	—
18.	13.xi.34	—	—	—	18.	13.xi.34	1	—	—
19.	14.xi.34	—	—	—	19.	14.xi.34	—	—	—
20.	15.xi.34	1	—	—	20.	15.xi.34	—	—	—

It may be seen that an apterous viviparous female can give rise to males, oviparous and apterous viviparous females. Consequently in *A. chloris*, there is no sexuparous form but apterous viviparous females, many generations from the fundatrix, respond almost immediately to the environmental conditions which dictate the form of the progeny. In this experiment the light conditions favouring the amphigonae continue for nine days. Since viviparous and oviparous females only occur together in tins 12 and 16, these individuals indicate (ignoring the solitary male) the extreme limits of the influence of the nine days of seven-hour lighting; and since the latter cause oviparous females to arise during a period of five or six days, it appears that at this temperature three or four days of this stimulus must be applied before oviparous female progeny can occur. It also appears that all embryos are not affected by the light conditions (directly or indirectly), for otherwise oviparous individuals would have begun to appear on the fourth or fifth day of the experiment. It may be concluded, therefore, that oviparous females cannot be produced from embryos within (at this temperature) eight or nine days of being laid.

The solitary male which was laid on the sixth or seventh day of the experi-

ment occurred many days before the earliest oviparous females. Males, therefore, can be produced from embryos which are too far developed to be capable of development into oviparous females.

A Further Experiment on the Production of Amphigonae in One Generation.

Another experiment was made on the influence of light on the progeny of individual apterous viviparous females. A slight modification of the normal technique was adopted, the aphids being reared, not in tins, but in 8-cm. glass tubes, which were maintained at a high humidity, by placing damp blotting-paper at the bottom of each tube and some damp cotton-wool at the open end. The experiment was conducted at a variable temperature which averaged 20° C. (based on two-hour readings).

Six apterous viviparous females of the thirty-sixth F.G. of *Line G*.1. were isolated and submitted to the following light conditions :—

A.1. *and A*.2. (an adult and a fourth-stage nymph respectively) were kept under continuous artificial light.
B.1. *and B*.2. (both adults) were kept in continuous darkness.
C.1. *and C*.2. (an adult and a fourth-stage nymph respectively) were subjected to seven hours artificial light each day (seventeen hours darkness).

The artificial lighting was from a 100-watt electric bulb. The progeny laid by each female each day were reared separately under the light conditions in which they were laid.

The six females were isolated on the 13th March, 1935. Of the two fourth-stage nymphs, *A*.2. became adult on the 15th and *C*.2. on the 14th. The forms of the offspring are given on p. 178.

In this experiment *A*.1. and *A*.2. are controls and it may be seen that these individuals gave rise to apterous viviparous females only. In *B*.1. and *B*.2. a few males arose between the 20th and 22nd, as a result of conditions of continuous darkness, but thereafter only apterous viviparous females occurred. In *C*.1. and *C*.2., on the other hand, the seven hours artificial light caused males to appear from the 19th and oviparous females from the 20th, the appearance of viviparous females being completely inhibited after the 20th.

The Occurrence of Males.

In the experiments which have been described in this paper, males occurred but rarely and some explanation of this fact should be attempted. It has been stated that in nature males begin to arrive earlier than the oviparous females, but that the latter continue to appear for some while after the males are all mature. It would seem, therefore, that between the light-temperature complex which favours the parthenogenetic individuals and that which favours the oviparous females is a set of environmental conditions which favour the male form. Now in the experiments which have been described here, the light conditions used were extreme, consisting of continuous artificial light, continuous darkness and seven-hours light a day. If, as seems probable, the conditions producing males lie within narrow environmental boundaries, it is not surprising that the drastic conditions to which the various lines were subjected rarely permitted males to arise. The " drastic " nature of the seven-hours light conditions becomes increasingly clear when one considers that adult

Date laid	Form of Adults			Date laid	Form of Adults		
	Apt. viv. ♀♀	Oviparous ♀♀	♂♂		Apt. viv. ♀♀	Oviparous ♀♀	♂♂
A.1.		Continuous Artificial Lighting					*A*.2.
14.iii	3	—	—				
15.iii	2	—	—	15.iii	1	—	—
16.iii	4	—	—	16.iii	4	—	—
17.iii	1	—	—	17.iii	—	—	—
18.iii	—	—	—	18.iii	1	—	—
19.iii	—	—	—	19.iii	1	—	—
20.iii	1	—	—	20.iii	—	—	—
21.iii	3	—	—	21.iii	3	—	—
22.iii	—	—	—	22.iii	1	—	—
23.iii	2	—	—				
24.iii	5	—	—				
25.iii	—	—	—				
26.iii	1	—	—				
27.iii	2	—	—				
B.1.		Continuous Darkness					*B*.2.
14.iii	4	—	—	14.iii	3	—	—
15.iii	3	—	—	15.iii	3	—	—
16.iii	1	—	—	16.iii	2	—	—
17.iii	—	—	—	17.iii	1	—	—
18.iii	—	—	—	18.iii	—	—	—
19.iii	—	—	—	19.iii	—	—	—
20.iii	1	—	1	20.iii	1	—	—
21.iii	1	—	—	21.iii	—	—	—
22.iii	1	—	3	22.iii	1	—	1
23.iii	—	—	—	23.iii	—	—	—
24.iii	2	—	—	24.iii	2	—	—
25.iii	3	—	—	25.iii	1	—	—
				26.iii	—	—	—
				27.iii	2	—	—
				28.iii	—	—	—
				29.iii	1	—	—
C.1.		Seven Hours Light a Day					*C*.2.
14.iii	4	—	—	14.iii	3	—	—
15.iii	4	—	—	15.iii	3	—	—
16.iii	2	—	—	16.iii	1	—	—
17.iii	—	—	—	17.iii	1	—	—
18.iii	—	—	—	18.iii	—	—	—
19.iii	1	—	2	19.iii	—	—	—
20.iii	—	1	1	20.iii	1	—	4
21.iii	—	—	1	21.iii	—	1	—
22.iii	—	2	—	22.iii	—	—	2
23.iii	—	—	—	23.iii	—	2	—
24.iii	—	1	—	24.iii	—	2	—
25.iii	—	2	—	25.iii	—	1	—
26.iii	—	2	—	26.iii	—	—	—
27.iii	—	—	—	27.iii	—	2	—
28.iii	—	1	1	28.iii	—	—	—
29.iii	—	2	—	29.iii	—	2	—

oviparous females are already present in the field on the 1st October, when the length of day from sunrise to sunset is 11 hours 37 minutes.

Summary.

An account of the results obtained from a number of experiments concerned with the factors which induce and inhibit the appearance of the different forms of *Aphis chloris* Koch is given. There are five forms of this aphid—the fundatrix, the apterous viviparous female, the alate viviparous female, the male and the oviparous female.

That the alate viviparous females are not essential to the cycle is demonstrated by a line, beginning from a fundatrix and ending with amphigonae, during the course of which no alatae occurred. It follows that alatae occur as a result of particular environmental conditions.

Evidence is given to show that the repeated " overcrowding " of *Aphis chloris* resulted in the repeated appearance of alatae. No temperature was found which favoured the appearance of alatae. It is concluded that " overcrowding " is the environmental factor causing the appearance of alatae, and this is interpreted as being a nutritional factor.

It is shown that a line of aphids may be continued for as long as seventy-seven filial generations (and probably indefinitely) without any amphigonae arising, and it follows that the appearance of the amphigonous generation is not predetermined for any particular generation from the fundatrix, but is essentially a result of environmental forces.

Results of an experiment are given in which nine lines derived from nine sister apterous viviparous females (thirty-fifth filial generation from a fundatrix) are subjected to various temperature and light conditions. It is shown that temperature and light conditions are two important environmental factors influencing the form of *Aphis chloris* : high temperatures and many hours of exposure to light result in a line remaining parthenogenetic and low temperatures and few hours of light exposure cause the appearance of the oviparous form; further, that these two factors are closely related, so that the effect of any particular temperature will vary according to the light conditions and *vice versa.*

An experiment is recounted in which four lines beginning from fundatrices are subjected to the conditions found most favourable for the production of oviparous females in the previous experiment. A comparison of the results obtained in the corresponding lines of the two experiments shows that, whilst the same results are finally attained, many more generations are required in the lines started from fundatrices. It is concluded that there is a further factor influencing the form of *Aphis chloris.* The nature of this " time factor " is discussed.

It is shown in two experiments that an apterous viviparous female can be induced to lay apterous viviparous female, male and oviparous female offspring, the nature of the progeny (parthenogenetic or amphigonous) being determined purely by the environmental conditions under which the parent female is kept. This result is in opposition to the customary belief that at least two generations must pass before suitable environmental conditions can produce amphigonous individuals, and demonstrates the absence of a " sexuparous form " in *Aphis chloris.*

Males seldom arose in the experiments recounted, due, it is suggested, to the " drastic " conditions under which the lines were maintained, these conditions

being very favourable to the viviparous females, or at the other extreme, to the oviparous females. Evidence from the field is given to support the view that the environmental conditions favourable to the males lie between those favouring the viviparous females and those favouring the oviparous females.

Literature.

There is a very considerable number of papers dealing with the question of the factors affecting the form of aphids, or containing some information bearing on the question. The brief list which follows consists of important papers, most of which have an extremely long bibliography:

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